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REVIEW

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Tracking animals in freshwater with electronic tags: past, present and future

Steven J Cooke^{1*}, Jonathan D Midwood¹, Jason D Thiem¹, Peter Klimley², Martyn C Lucas³, Eva B Thorstad⁴, John Eiler⁵, Chris Holbrook⁶ and Brendan C Ebner⁷

Abstract

Considerable technical developments over the past half century have enabled widespread application of electronic tags to the study of animals in the wild, including in freshwater environments. We review the constraints associated with freshwater telemetry and biologging and the technical developments relevant to their use. Technical constraints for tracking animals are often influenced by the characteristics of the animals being studied and the environment they inhabit. Collectively, they influence which and how technologies can be used and their relative effectiveness. Although radio telemetry has historically been the most commonly used technology in freshwater, passive integrated transponder (PIT) technology, acoustic telemetry and biologgers are becoming more popular. Most telemetry studies have focused on fish, although an increasing number have focused on other taxa, such as turtles, crustaceans and molluscs. Key technical developments for freshwater systems include: miniaturization of tags for tracking small-size life stages and species, fixed stations and coded tags for tracking large samples of animals over long distances and large temporal scales, inexpensive PIT systems that enable mass tagging to yield population- and community-level relevant sample sizes, incorporation of sensors into electronic tags, validation of tag attachment procedures with a focus on maintaining animal welfare, incorporation of different techniques (for example, genetics, stable isotopes) and peripheral technologies (for example, geographic information systems, hydroacoustics), development of novel analytical techniques, and extensive international collaboration. Innovations are still needed in tag miniaturization, data analysis and visualization, and in tracking animals over larger spatial scales (for example, pelagic areas of lakes) and in challenging environments (for example, large dynamic floodplain systems, under ice). There seems to be a particular need for adapting various global positioning system and satellite tagging approaches to freshwater. Electronic tagging provides a mechanism to collect detailed information from imperilled animals and species that have no direct economic value. Current and future advances will continue to improve our knowledge of the natural history of aquatic animals and ecological processes in freshwater ecosystems while facilitating evidence-based resource management and conservation.

Keywords: Acoustic telemetry, Biotelemetry, Coded tags, Passive integrated transponder, Radio telemetry

Background

Freshwater ecosystems around the globe face many threats and stressors [1-4], which have collectively led to dramatic reductions in freshwater biodiversity for a range of taxa [5,6]. Human activities are the primary source of these multiple stressors [7], such that Strayer and Dudgeon [8] eloquently describe what they call, 'the collision between humans and biodiversity in freshwater

ecosystems.' Freshwater ecosystems provide vital resources for human beings (including water for drinking and irrigation, food, electricity and transport) and demands for freshwater have risen dramatically over the last century. The 125,000 species of freshwater animals that have been described represent 9.5% of all known animal species on the planet (including one-third of all vertebrate species), even though fresh waters cover just 0.8% of the Earth's surface [6,9], emphasizing that freshwater ecosystems are hotspots for biodiversity [8]. Unfortunately, owing to the proximity of human population centres to sources of freshwater and the associated

* Correspondence: steven_cooke@carleton.ca

¹Fish Ecology and Conservation Physiology Laboratory, Department of Biology, Carleton University, 1125 Colonel By Dr., Ottawa, ON, Canada
Full list of author information is available at the end of the article

demands on this resource, these systems are also hotspots for endangerment [6,8]. Given the immense ecosystem services provided by freshwater ecosystems [10], the importance of the animals that occupy these waters [11], and the livelihoods and well-being of the human beings that depend upon freshwater ecosystems [12,13], there is a need to understand the biology of freshwater animals.

Basic life history information (including habitat requirements, migratory routes, foraging and reproductive sites, dispersal and home-range characteristics) is fundamental to understanding animals in relation to their environment, and when studied in the context of responses to human activities, provides resource managers and conservationists with practical knowledge to make informed decisions. However, studying macroscopic animals in freshwater ecosystems comes with its own unique set of challenges. Extreme depths, and high turbidity, discharge or current speed, ice cover, habitat complexity, and macrophyte density constrain the ability to view and collect freshwater animals. Additional constraints are imposed by the fact that some animals are small, cryptic or highly mobile. Although certain types of behaviour and physiology can be easily studied in captivity, relying solely on this type of study can be misleading since such studies fail to mimic natural scenarios involving complex interactions among multiple species and large-scale processes.

Today's field biologists have a variety of tools for studying animals in the natural environment, but given the challenges with visual observation in aquatic habitats, electronic tagging technology is regarded as one of the most effective means of studying the behaviour and ecophysiology of animals in their natural environment [14]. A variety of electronic tagging tools have been used in freshwater for the study of vertebrates and some of the larger invertebrates (summarized in [15-18]; See Table 1). Active telemetry tools that remotely transmit information between a transmitter and receiver, including radio and acoustic telemetry, and passive tools, such as passive integrated transponders (PIT tags), have been applied to a variety of freshwater taxa (Figure 1). Archival devices that record information from sensors (such as temperature, pressure, activity) that can be downloaded onto retrieving devices (also known as biologging) are also increasingly common in freshwater systems. These types of sensor have also been used extensively with active telemetry tools to enhance information collected regarding animal locations.

Despite the breadth of current telemetry technology, there are still many challenges associated with using electronic tags to study freshwater species. These range from the problem of attaching devices to animals, to the technical performance of the electronic technology, and

methods of analyzing data. By considering historical developments that have led to our contemporary electronic tagging toolbox, it is possible to identify specific constraints and technical gaps that still exist and provide the foundation needed to foster future advances. To that end, the objective of this synthesis is to consider the past, present and future of electronic tagging and tracking techniques and technology. In order to narrow the scope of the review and focus on environments that share similar challenges, we focus on animals found in freshwater systems, including fish, mammals, reptiles, amphibians and invertebrates (mostly molluscs and arthropods) that are sufficiently large to be studied with electronic tags. We exclude all birds, since most associated tracking studies for birds focus on large-scale migrations. We include diadromous fish (but only their freshwater phase) as well as mammals that spend significant time in freshwater (for example, muskrats, manatees). This is not intended to be an exhaustive review. Rather the information presented represents the collective knowledge and perspectives of the authors with experience in using a variety of electronic tagging technologies, in different regions, and on different taxa.

Key developments in freshwater tracking

The creation and use of new technologies, methods and approaches is a gradual process. As such, many of the key developments are a culmination of innovation and discovery rather than a single discovery (or paper). Table 2 presents a list of key telemetry technologies used to study freshwater animals in the wild, and their associated strengths, weaknesses and typical applications.

Reduction in tag size

The progression of smaller and more efficient electronic components has been a major advance for aquatic telemetry, making it possible to reduce tag size substantially, and tag and track a wider range of species and life stages. Miniaturization has also made it possible to increase the capabilities of transmitters used on larger animals in terms of operating life, reception range and environmental and physiological sensors. Like many technologies, this has been a gradual process, and many of the advances in the 1970s set the stage for future work. Specific details in journal articles were often relegated to a few lines in the methods section, but the overall trend can be inferred from the steady increase in telemetry papers focused on habitat selection and movement patterns in smaller species and juvenile life stages of fish [63,64], and increasingly smaller nonfish taxa, such as some amphibians (black-bellied salamanders [65]) and invertebrates (crayfish [66]). Radio tags as small as 0.25 g, acoustic tags as small as 0.30 g, and PIT

Table 1 Summary of the various technologies used for tracking animals in freshwater with a brief summary of strengths, limitations, and common applications

Technology	Summary of technology and techniques	Strengths	Limitations	Applications
Acoustic telemetry; manual tracking	Uses a transducer to convert electrical energy to acoustic energy that is detected by an underwater hydrophone	Deep water (>20 m)	Hydrophone must be submerged in water	Some applications in FW
	Animals usually tracked by boat using bearings and triangulation	Can provide detailed movement data depending on tracking method and conditions	Ineffective in shallow or turbulent water	Mostly for fish, some use with alligator, FW mammals and elasmobranch
	Not suitable for transmitters with long pulse interval (time between pulses)		Interference from macrophytes and noise (for example, boats, entrained air)	
Acoustic telemetry; fixed stations	As above	Can be deployed as gates, grids, or arrays to monitor animal movements for long periods, including under ice	Generates large datasets	Widespread use in FW
	Autonomous or cabled hydrophones and associated loggers store time-stamped data when tagged animals enter reception zone	Multiple stations can provide precise two or three-dimensional tracks of animals	Requires significant post-processing and analytical efforts (can be challenging to recover data with some systems)	Mostly on fish, some use with mammals that move between marine and FW environments
		Some systems provide real-time data transmission	Interference from macrophytes and noise (for example, boats, entrained air)	
Radio telemetry; manual tracking	Emit electromagnetic energy in the radio frequency range (usually in the VHF band between 30 and 300 MHz)	Shallow water (<10 m)	Deep water (>15 m)	Widespread in FW
	Signals detected by antennas (aerial or underwater) and a receiver (some have logging capability)	Low-conductivity (<500 $\mu\text{S}/\text{cm}$)	High conductivity Sensitive to localized interference	Fish and other taxa, especially amphibious species (for example, basking turtles, amphibians, some mammals)
	Tracking can occur from boat, vehicle, air, foot	Relatively inexpensive Functions in moving water and through ice as well as on land and in air		
Radio telemetry; fixed stations	As above	As above	Antennas visible, thus can attract vandals	Widespread use in FW
	Fixed stations with multiple antennas detect and log tags when in the vicinity of an antenna	Suitable for long-term deployments	Not possible to obtain precise two-dimensional positions (mostly presence or absence in a given location)	Mostly used with fish
	Most often deployed in riverine systems to detect migration		Sensitive to interference Effectiveness dependent on local geomorphology and station placement [19]	
Passive integrated transponder telemetry; manual tracking	Integrated circuit chip and coil antenna that transmits a unique identity code when energized by a low-frequency radio signal (generally 125 to 400 kHz)	No battery (therefore long life)	Largely limited to shallow and restricted lotic systems owing to small detection range (usually <1 m)	Widespread use in FW

Table 1 Summary of the various technologies used for tracking animals in freshwater with a brief summary of strengths, limitations, and common applications (Continued)

	Detected using hand-held (usually in a backpack with wand waved in or above water surface while wading or walking on ice) or boat-mounted readers	Small	Multiple tags in the same location can prevent signal transmission	Mostly in small fishes, reptiles, amphibians and invertebrates
		Inexpensive	Detection range depends on tag orientation relative to the reader	
Passive integrated transponder telemetry; fixed stations	As above	No battery (therefore long life)	As above	Widespread use in FW
	Antennas deployed in systems that record the time and unique ID of a given tag detection	Small	Remote stations require power source to function	Mostly for fish
	A variety of antenna designs, mostly for small lotic systems, fishways or other areas where animals congregate	Inexpensive		
Low-frequency electromagnetic telemetry	Similar principle as PIT tags, but tags are continually powered	Effective in areas with high noise levels where acoustic and radio may be problematic	Site-specific detection only	Limited use in FW
	Greater detection range on the order of several tens of metres (for example, [20,21])		Limited tag life	The few examples use fish in lowland rivers [20]
Combined acoustic radio transmitters	Both acoustic and radio output modules can either transmit simultaneously or, if dynamic, can switch between the two	Works in marine and FW	Large devices	Some use in large diadromous fish species and marine mammals that move between marine and fresh waters
	Switching driven by environmental cues (depth or conductivity) [22]	Works for animals that use a wide range of depths or move into higher conductivity waters	More expensive than either radio or acoustic tags	
Archival tags (no transmitting capability)	Biologging tags (for example, data storage tags, time-depth recorders, archival geolocation tags)	Continuous monitoring of desired parameter (for example, temperature, depth)	Require tag recovery to download data from onboard memory	Some use in FW, mostly for logging temperature, depth, geolocation, and other environmental parameters (especially for ectothermic animals)
	Do not transmit data remotely			Occasionally log physiological information (for example, acceleration, heart rate)
	Always equipped with some form of sensor			
Communicating histogram acoustic transponders and business card tags	Hybrid loggers and transmitters, first logging data to memory and later transmitting data when interrogated by a receiver	Useful for wide-ranging fishes that have low recapture probabilities but return to download sites [23]	Reasonably large	Not applied in FW to our knowledge (mostly marine applications)
	Business card tags are a variant where the logging function actually serves as a mini acoustic receiver and can log other tagged animals that it encounters [24]		Expensive	
			Some versions require that tags are retrieved to download data	
Smart position-only tag with real-time GPS	Satellite platform transmitter which identifies tag location by real-time uplinks to orbiting Argos satellites whenever tag breaches the water surface (some variants may include archival capability rather than only transmitting in real time)	Real-time positioning	Relatively expensive	Mostly marine
		Provides information on broad-scale movement of animals (for example, ocean basin scale)	Individual must breach water	Some use in large FW animals that surface (for example, alligators, manatees)
			Limited to large animals	

Table 1 Summary of the various technologies used for tracking animals in freshwater with a brief summary of strengths, limitations, and common applications (Continued)

		Detailed records of environmental conditions experienced		
Archival pop-up satellite archival transmitter tags	Tags programmed to jettison at a given time or when tags experience a specific event (for example, fail to change depth for a specified period of time) at which time they float to surface and transmit summary data or packets to satellites	Provides information on broad-scale movement of animals (for example, ocean basin scale)	Most release links based on corrosive link, switched on via applied voltage and require sea-water to function	Mostly marine
	Geopositioning commonly based on light levels	Detailed records of environmental conditions experienced	Limited to large animals	Most FW applications involve diadromous animals tagged during FW phase with pop-off scheduled for when they are in marine systems
	Can also log depth and temperature		Relatively expensive Tags and downloading technology not always reliable, needs further refinement	Exception: studies on FW porpoises [25]

FW, freshwater; GPS; global positioning system; VHF, very high frequency.

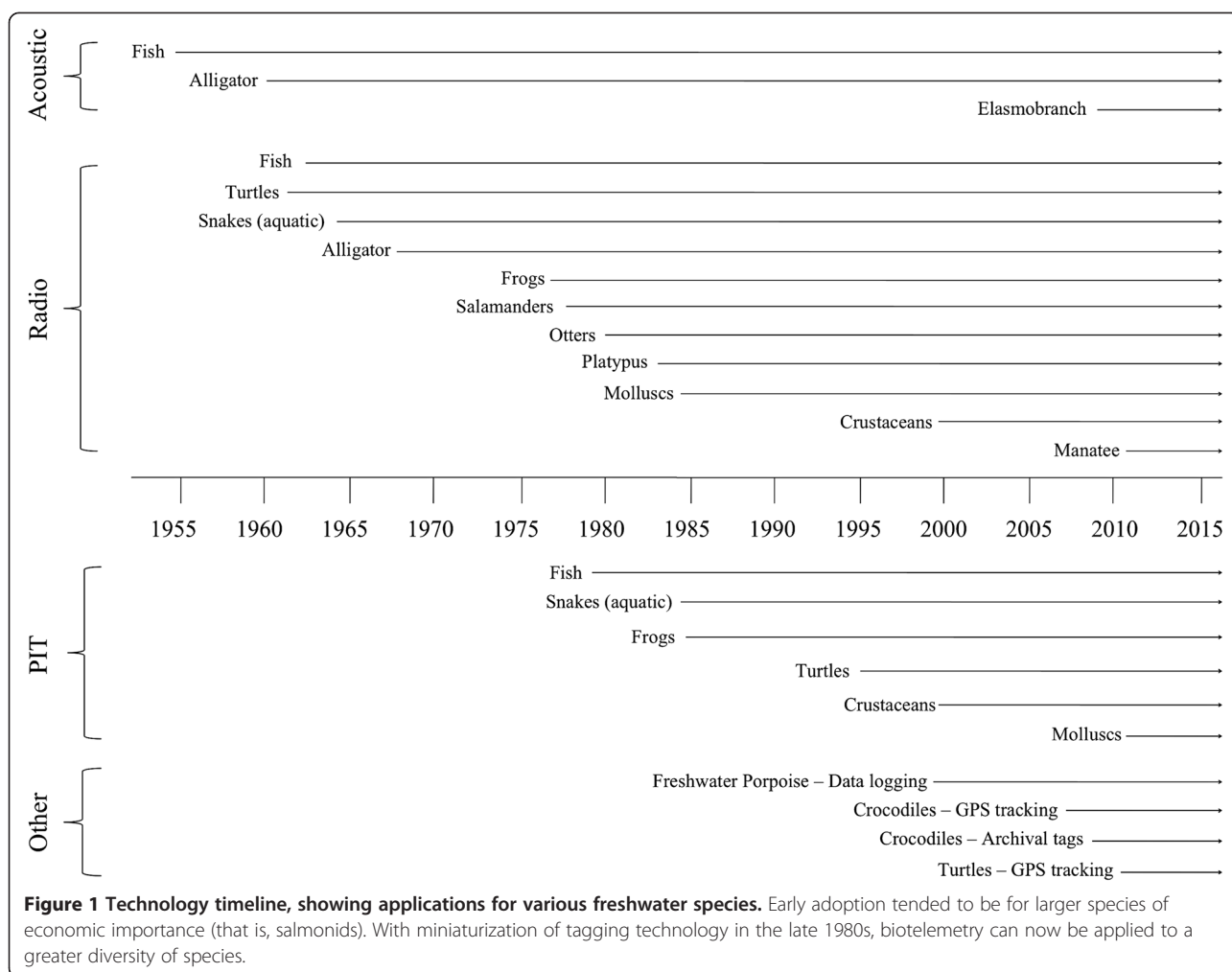
tags as small as 10 mg are commercially available at the time of publication.

Coded signals

The advent of coded transmitter signals is a technical advance that made a major impact on the study of freshwater animals. Prior to the mid-1980s, most telemetry studies were limited to small numbers of individuals (usually <40) in relatively confined areas. The need for more quantitative data on large aggregates of fish, such as the timing and number of returning adult salmon and their migration through entire watersheds [67], made it necessary to develop new approaches for dealing with large numbers of wide-ranging individuals. Because of the commercial importance of Pacific salmon returns in north-western North America, funding was often available to support these developments, which subsequently had transferable benefits for studying other species. In addition to increasing the number of frequencies being monitored, transmitters encoded with simple, audibly distinguishable signal patterns (for example, single, double and triple-pulsed transmissions) or varying pulse rates (for example, 60 vs. 90 pulses per minute) were used to increase the number of unique individuals that could be identified. By the late 1980s, more sophisticated signal patterns were adopted, which together with receivers able to distinguish the encoded signal, dramatically increased the number of individuals that could be identified [42]. For acoustic applications, the advent and application of code division multiple access technology enabled multiple animals to be detected simultaneously [51]. Coded tags are now taken for granted, but represented a significant innovation for freshwater systems.

Stationary tracking

Passive telemetry systems (where receivers are deployed at stationary locations to record tagged animals that come within range of an antenna or hydrophone) in freshwater were based on coded transmitter technology. Receivers deployed throughout watersheds, and linked via satellite to relay data back to a central processing facility, were first deployed for Pacific salmon to study their upstream spawning migration [67]. Receivers could be programmed to scan a variety of frequencies and antennas, either sequentially or simultaneously (for example, using digital spectrum processing [68,69]), sometimes in an intelligent manner such that when fish were present they would prioritize ‘listening’ on a given antenna or frequency [19]. Stationary acoustic receiver systems were first used in marine systems [70,71] and are now routinely applied in inland waters, especially large rivers, lakes and reservoirs to assess migration patterns [72]. Hydrophones, coding and signal-processing advances mean that freshwater animals can now be tracked in river systems that were too turbulent and noisy for previous acoustic systems [71,73-75]. Autonomous omnidirectional acoustic receiver-loggers can be deployed in arrays to efficiently record diadromous fishes migrating between freshwater and marine systems, by enabling the same individuals to be employed in both habitats. This is even possible for small fish, thanks to the availability of relatively small transmitters compared with the combined acoustic and radio tags (CARTs) previously available). This technology, when used in combination with archival tags, has enabled researchers to describe detailed behaviour of steelhead trout during the riverine and oceanic migration [76]. Many of the passive



acoustic systems can be deployed subsurface and operate autonomously for extended periods (over a year) without requiring additional maintenance and battery changes, which has allowed for continuous tracking of the behaviour of freshwater species [23,38]. Recent developments include links to communication systems (for example, satellites, cellular networks, underwater acoustic modems) to enable data collection without retrieval of equipment. Large-scale acoustic telemetry arrays have now been installed in the Laurentian Great Lakes and many large river systems around the globe, and are based on international collaborations in transboundary waters focussing on wide-ranging animals. If configured with a minimum of three time-synchronized hydrophones, hyperbolic navigation using time difference in signal arrival can be used to generate highly accurate and precise animal positions [42,70]. To date, there are only a few published examples using such technology in freshwater, which have focused on questions of spatial distribution and variation in temporal activity [26,27,77], but many projects using that approach are now under-

way, including some that use relatively inexpensive technology to look at simultaneous fine-scale movements of multiple individuals [78]. Passive PIT telemetry arrays (discussed below) have also provided similar benefits. Development in antenna technology robust to dynamic river and stream conditions [32] has enabled longer-term field deployments.

The technical contributions noted above have led to a number of important and unique ecological advances. Unlike many marine and terrestrial ecosystems, rivers are by nature linear. The work of Fausch *et al.* [32] was instrumental in discussing some of the problems associated with trying to conduct ecological research broadly within the 'riverscape'. Telemetry applications provide a rare exception; a research method that actually capitalizes on the physical structure of dendritic freshwater ecosystems in capturing movement processes. For this reason, stationary receiver-loggers (often termed automatic listening stations) of radio, acoustic and inductive coupling forms have been deployed along many reaches of rivers to determine rates of movement and survival

Table 2 Summary of key constraints (categorized by abiotic, anthropogenic, environmental/habitat, and biotic) associated with using electronic tags to study animals in freshwater systems, existing technical solutions, and additional technical needs that need to be addressed to improve equipment performance and science outcomes

Category	Condition	Constraint	Existing technical solutions	Additional technical needs
Abiotic	Ice cover in lentic systems	In some regions ice cover for part of the year impedes access the water Modifies signal properties (for example, via reflections, noise) May create problems during breakup by moving or damaging equipment	When ice conditions are safe animals can be tracked through the ice with radio receivers on foot (skiing, snowshoeing) or driving (for example, snowmobile) Acoustic receivers can be deployed below ice but must be moored so that they are not dragged during ice breakup (for example, do not use surface buoys [26])	Little information on acoustic performance under ice but some evidence of noise from cracking or shifting reducing detections (Mike Parsley, personal communication) Understand the performance of acoustic telemetry (especially for logging and automated positioning) under the ice [27]
Abiotic	Ice dynamics in lotic systems	Winter ice dynamics pose problems for gear deployed in water due to potential damage (for example, PIT antennas, hydrophones [28]) Loss of reception associated with noise and physical obstruction (especially acoustic telemetry [31])	Radio telemetry is favoured for tracking [29,30] Flatbed PIT antennas reasonably robust to ice processes [32] In small streams, use mobile PIT antennas through the ice [33]	For PIT and acoustic systems there is need for antenna and receiver designs that are not subject to ice damage
Abiotic	Shallow water	Exceptionally shallow water (for example, 0 to 30 cm or even ephemeral systems, like billabongs) can expose underwater hydrophones and make manual acoustic tracking nearly impossible [34]	Radio telemetry and mobile PIT antennas can be used in shallow water Care must be taken not to disturb or chase animals being tracked	Limitations due to physics and physical constraints unlikely to be overcome with technology
Abiotic	Deep water	Deep water attenuates radio signals [35,36] and makes use of radio transmitters and PIT tags ineffective for positioning (in the latter case by virtue of the current difficulty of deploying PIT antennae at depth, though technically feasible if linked <i>in situ</i> with waterproofed logger and power supply)	Acoustic telemetry performs well in deep water but positioning accuracy will depend on depth Can use CART tags [22] A downrigger device has been developed that enables tracking of radio-tagged fish at depth, but has limited reception zone [37] Low-frequency radio tags can improve performance in deep water [35] as can use of more powerful batteries or stronger transmitter output [36]	Unlikely that technical developments will improve performance of radio and PIT systems in deep water
Abiotic	Thermocline	Thermoclines can impair the performance of acoustic transmitters [38,39], but radio transmitters are unaffected (aside from the fact that thermoclines often occur at depth)	Hydrophones can be placed both above and below thermoclines to improve reception, or at the same level as the fish being tracked if they do not frequently cross the thermocline Rarely is performance so degraded that acoustic detections are not possible, but may impede ability to achieve fine-scale positioning	Unlikely that technical developments will entirely address this issue with acoustic tags
Abiotic	High flows, currents and turbulence	High water flows in riverine systems or from lentic currents (creating noise on hydrophones) and associated turbulence and entrained air (even in low flows) can impede the performance of acoustic telemetry systems [40]	Increasing the density of acoustic receivers can improve detection probability [40]	There is need for technical developments further refining code detection and noise filtering in acoustic telemetry systems deployed in high flows, currents and turbulence

Table 2 Summary of key constraints (categorized by abiotic, anthropogenic, environmental/habitat, and biotic) associated with using electronic tags to study animals in freshwater systems, existing technical solutions, and additional technical needs that need to be addressed to improve equipment performance and science outcomes
(Continued)

			Fixed acoustic receiver station deployment innovations enable their placement in large rivers [41]	Shielding of hydrophones may help to reduce noise (Dale Webber, unpublished data)
			Radio telemetry is unimpeded by such conditions	
			Fixed PIT systems may be difficult to maintain in high flows (get washed out)	
Abiotic	Turbidity	High turbidity (especially if associated with suspended matter) can impair performance of acoustic systems [42]	Acoustic systems usually perform well except in extreme turbidity	Need to develop alternative ways of positioning animals with sensors that do not require light levels (that is, PSATs)
		Makes use of light sensors to position animals ineffective (for example, loggers or PSATs)	Radio and PIT are much less affected	
Abiotic	Conductivity	High conductivity can severely attenuate VHF and HF radio signals in particular but can also reduce performance of acoustic telemetry systems [34]	The extent of radio signal attenuation varies by radio frequency such that choice of lower frequencies (for example, 30 MHz) can improve performance [43,44]	Innovations in the marine realm for devices that function well in high salinity (and thus high conductivity) potentially benefit freshwater research
			Conductivity presumably also influences PIT system performance [45]	
			Compared with radio, acoustic performance is relatively unaffected by high conductivity [33,46]	
			Can use CARTs [22]	
Abiotic	Salinity	Saline environments have very high conductivity and make VHF and HF telemetry unusable (as above)	In saline environments, PSATs based on corrosive releases that enable tags to be jettisoned can be used	Development of PSAT releases that work in freshwater would provide new tracking opportunities
		High salinity has an effect on how much sound energy water absorbs [47], which is relevant for acoustic tracking	Corrosive releases do not work in low-salinity environments; limits use of PSATs in inland systems	
			Most inland systems would not have problems with radio attenuation or acoustic energy absorption due to salinity	
Abiotic	Air-water interface	Some animals move in and out of water frequently (for example, turtles) despite being primarily aquatic, which leads to varied signal strength for radio tags and no signal for acoustic tags when in the air	Most studies of animals at the interface use radio telemetry although satellite and GPS tags can also be effective	Unlikely that technical solutions will address these issues
			Acoustic tags can still be used to quantify timing and duration of out of water activities (for example, basking in turtles)	
			CART technologies can be used	
Anthropogenic	Human activity and vandalism	In areas with human activity, some telemetry infrastructure is conspicuous and can attract vandals [48]	Acoustic receivers, if deployed at depths and using gear that the public cannot easily reach, are usually safe from vandals	Development of less conspicuous deployments for radio and PIT gear, such as autonomous underwater antennas and receiving systems (as is common in acoustic telemetry)
		Swim-through PIT loops, with the top edge above the water surface should not be deployed where boats occur	Most fixed-radio and PIT tag antenna arrays (unless in controlled access areas) are subject to vandalism even when using 'vandal-resistant' gear	

Table 2 Summary of key constraints (categorized by abiotic, anthropogenic, environmental/habitat, and biotic) associated with using electronic tags to study animals in freshwater systems, existing technical solutions, and additional technical needs that need to be addressed to improve equipment performance and science outcomes
(Continued)

			(for example, fixed and locked boxes [48])	
			Miniaturization of power systems and autonomous receivers has helped to deploy receivers out of sight	
			Labeling the equipment with information on content, purpose and value of equipment may reduce likelihood of vandalism in some areas	
Anthropogenic	Human infrastructure and construction materials	Human infrastructure (for example, fishways, dams) are often studied using electronic tags but the construction materials (for example, concrete, metal), operations (for example, entrained air, high flows), and electromagnetic activity (for example, from hydro wires) can interfere with radio, PIT and acoustic systems	Underwater radio antennas can be used in areas near electrical infrastructure to reduce interference [49]	Continued development of equipment that is robust and shielded from electromagnetic activity
		Background radio noise over a wide range of frequencies (for example, communication systems and electrical devices)	Many efforts have been devoted to developing acoustic systems that can work around infrastructure	Development of improved radio telemetry coding systems
			PIT arrays work well in such areas but need to be cautious around metal surfaces	
			Use existing coding systems to avoid background interference	
			Prior to starting a study, identify frequencies that are prone to high levels of interference in your area	
Anthropogenic	Noise	Boat traffic, waves, rain and biological noise can all make detection of acoustic signals difficult	Radio and PIT unaffected unless electrical interference from vessels (including electromagnetic noise interference from tracking boat [22])	Improvements in coding to improve performance when signal to noise ratio is not optimal for acoustic systems
		For example, rainfall can produce or increase noise levels of 15 to 25 dB in the water column [47]	Much less biological noise in freshwater than marine systems, so not a problem in most situations	Conducting detailed system-performance tests under different conditions needed to determine acoustic system efficiency (for example, in a shipping canal)
Environment or habitat	Remote areas	Many inland regions are remote, creating challenges for tending and operating electronic equipment [48,50]	Solar panels and special battery banks have provided power in remote locations for fixed stations (mostly radio and PIT systems [50])	Need for technological improvements to address challenges with maintaining systems in winter or damp environments (for example, better weatherproofing of equipment [48])
			Satellite connections enable data to be retrieved and receivers to be configured from afar (already exists for radio [51] and recently developed for acoustic systems with a surface cable and GPS or cell interface)	More remote communication options to enable servicing from afar
			Aircraft-mounted antennas can be used for radio tracking animals over great distances in remote locales [52,53]	Batteries that last longer or systems that require less power

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(Continued)

Environment or habitat	Habitat configuration	Geomorphological configuration of habitats (for example, type and configuration of banks, fjords, roughness of substrate, type of substrate) can influence performance of both acoustic [40,54] and radio telemetry [55]	Increasing density of acoustic receivers can improve detection probability in some areas (for example, such as near banks in rivers or areas with high levels of substrate roughness [56]) Manual radio tracking can be confusing around some habitats (for example, rock walls) such that practice is needed to become efficient at locating tags	Need for additional studies to better understand how habitat configuration influences detection of radio and acoustic telemetry signals
Environment or Habitat	Cryptic habitats	Some animals make use of cryptic habitats that make tracking difficult (for example, crayfish and mammals can use burrows [57]; some fish hide under rocks [37]) due to signal attenuation and deflection; acoustic telemetry ineffective in such situations Radio telemetry and PIT tracking possible if animals are not too deep into cover	Use tags that are as powerful as possible (for example, high-output radio tags)	An intrinsic challenge that cannot be easily overcome with technology Efforts should focus on training of team members to track in such environments
Biotic	Macrophytes	Macrophytes can impede sound when using acoustic telemetry [34] and can foul external telemetry transmitters [58]	Unclear if specific frequencies or other characteristics of acoustic telemetry systems would improve performance in dense macrophyte beds Radio telemetry performs well in dense macrophytes Use internal tag implantation in animals that are in regions with lots of macrophytes	Need for rigorous testing of acoustic telemetry gear in and around macrophytes to identify ideal frequencies for local conditions
Biotic	Animal damage	Vermis of various types (mostly mammals such as muskrats or insects such as ants) can chew through wires for cabled systems (including cabled acoustic arrays [59]) or damage-sensitive electronics [48]	Wires can be protected with sheaths and various pest control strategies can be used (for example, pesticides in land-based fixed stations) External tags can be designed to minimize chewing by mammals (for example, was a problem for box turtles [60])	Further developments such that cabled systems are not needed Development of strategies for camouflaging and protecting wires and making gear sealed to prevent entry of insects
Biotic	Biofouling	Algae and molluscs (for example, <i>Dreissena</i> spp.) in particular can build up on underwater equipment, such as fixed hydrophones or underwater antennas, reducing performance [61] Fouling of external tags can reduce performance and burden tagged animals [62] Fouling of light sensors makes use of geopositioning tags in freshwater difficult	Underwater equipment such as hydrophones and antennas can be cleaned (for example, by divers) or various biofouling materials (for example, special paints [61]) can be used Tags (and antennas) can be placed internally [62]	Need for biofouling paints and materials that are minimally toxic Need for methods of geopositioning animals without light

CART, combined acoustic radio transmitter; GPS, global positioning system; HF, high frequency; PIT, passive integrated transponder; PSAT, Pop-up satellite tag; VHF, very high frequency.

[20,22,75,79,80] and along diverging paths to the sea to determine route selection [20,81]. While the use of acoustic telemetry arrays in marine environments has provided important spatial data for large-bodied marine fauna, there has been an even greater rate of return for investment in telemetry infrastructure in rivers. This is largely a function of the contained and branching nature of rivers, when compared with the unconstrained shape of most marine areas in relation to the relatively limited range of acoustic receivers.

PIT telemetry

Passive integrated transponder telemetry has provided an affordable tool that enables researchers to study smaller individuals or juvenile life stages than is possible with radio and acoustic telemetry using both active and passive tracking. In addition, tags remain viable for long periods (years), owing to the lack of onboard batteries, allowing long-term tracking of individual fitness proxies, such as growth and survival [16,82-84]. Owing to the much shorter range (less than 2 m perpendicular to the antenna plane) than radio and acoustic transmitters, PIT telemetry has mainly been used in smaller systems. It is especially valuable in assessing fish movement through narrow passageways, such as fish passes [85] and streams [86,87], but is increasingly used in wider swim-through channels (30+ m × 0.8 m deep) using an array of tag readers. Passive systems yield high-quality long-term recording of large samples of animals at discrete locations [88]. Mobile PIT detectors (backpack and boat or trawl-mounted models for example [89]) have been developed as a less obtrusive method for studying the ecology of refuge-seeking or cryptic species of fish, invertebrates (for example crustaceans [90,91], molluscs) and amphibians [92]. One prominent innovation with PIT telemetry has been the ability to visit bird colonies to estimate predation on small fish (mostly salmonid smolts) by locating PIT tags on land [93]. Further, the cost of PIT tags remains about one hundredth of that of battery-powered radio and acoustic transmitters, facilitating large sample sizes with PIT telemetry.

Sensor tags

The incorporation of sensors into radio and acoustic transmitters and archival tags has provided novel insight into animal-environment associations and the energetic costs of different behaviours (for example, basking) and stressors (for example, fisheries interactions, fishway use). Some of the earliest sensors incorporated into electronic tags were simple activity or motion sensors that provided the status of a fish (that is, whether it is moving or stationary [94]). The success of these tags encouraged the development of other sensor types. Physiologically oriented sensors (for example, electrocardiography; electromyo-

graphy, acceleration) have been used primarily on fish [95,96]. Electromyography sensors incorporated in radio transmitters were developed in the 1970s to record opercular muscle activity or overall fish locomotor activity [97-99], and are today the most commonly used physiological sensor tool for studying energetics and migration in freshwater fish [17]. Electrocardiography or other cardiac metrics, such as heart rate (see [100] for review) have been used in radio (for alligators [101] and for fish [102]), acoustic (for fish [103]) and archival (for fish [104,105]) tags. Of late, acceleration loggers [105,106] and acoustic acceleration transmitters (SJC, unpublished data) have been used to assess temporal changes in energy expenditure and movement rate and are expected to grow in popularity for application in freshwater, akin to the uptake of this technology in terrestrial and marine applications [107,108]. Environmental sensors, particularly temperature and pressure (that is, depth [109]), have been used on a wide range of reptiles (for example, turtles [110]) and fish [111] and have been used in radio and acoustic transmitters and archival tags to link location with the environmental parameters measured by the sensors. Other environmental sensors linked to transmitters have also been designed to assess the range of key parameters, such as conductivity [112] and oxygen [113], that fish are exposed to during normal activity. Relatively cheap archival temperature tags now available on the market enable collection of long-term thermal information and large sample sizes, provided that the tags can be retrieved (for example, alligators [114], turtles [115], salmon [116]). Early sensor tags were developed by individual researchers, who would build the tags either themselves or in collaboration with engineers [112,117-119]. However, many of these sensors now represent 'standard' options for commercially available tags, and their use is greatly simplified. Collectively, these tools have provided novel insights in animal behaviour, energetics and physiology that would not be possible by simply measuring the location of an animal.

Integration of peripheral technologies

In addition to improvements specific to telemetry and logging equipment, advances in other, often unrelated, technologies have dramatically increased the options available to researchers and made them easier to adopt. For example, availability of low-cost GPS, some even integrated with receiving systems, has improved the positional accuracy and usability of the telemetry data collected (a vast improvement over drawing circles on a map [52]) allowing fine-scale assessment of movement. Uplink technology (for example, satellite, Wi-Fi, cellular, Bluetooth) and nonvolatile data storage has made it faster and easier to recover telemetry data from stationary tracking systems, particularly those in remote or inaccessible areas. Computerized databases have increased

the efficiency of data analyses, and links to the internet make the information easier to disseminate and widely available.

Tagging techniques

More so than in marine environments, significant effort has been devoted to the development and validation of various attachment and implantation procedures (including pre- and post-tagging care), particularly for fish (reviewed in [58,120,121]) but also for reptiles [122]. If the tags or associated tagging procedures result in altered behaviour, energetics, condition or survival relative to untagged conspecifics, then findings emanating from tagging studies may be biased or incorrect [28]. Most research efforts have focused on identifying the maximum tag burdens for a range of taxa (including turtles, fish and amphibians), testing and optimizing tagging techniques, assessing different tag types, [123,124], testing anaesthetics (for example, for turtles [125] and fish [126]), and identifying species- or taxon-specific challenges [120]. These challenges often relate to the composition, rigidity or permanence of an animal's outer surface in regard to externally tagging (for example, reptiles [122,127], an elasmobranch [128], a slippery fish [129], crayfish [91]) or physiological acceptance of foreign bodies following internal tagging [130,131]. Particularly in freshwater, fouling of external tags (for example, with macrophytes) and associated impacts on drag have led to innovations in internal surgical procedures [132] that have advanced tagging for marine fish. Indeed, many of the refinements in animal handling associated with the development of tagging procedures for freshwater fish have led to broader improvements in and attention to animal welfare for aquatic animals used in research [133].

Combining electronic tagging with other research methods

Although early studies focused largely on using electronic tags to identify habitat use and movements (that is, descriptive; reviewed in [15]), electronic tagging is increasingly being combined with other techniques and tools. Such advances have increased the complexity of questions that can be addressed and provide more mechanistic explanations of animal behaviour through hypothesis testing (reviewed in [134]). This can be accomplished with integrative studies that combine techniques in parallel (for example, a study that has a laboratory and field component), by obtaining nonlethal biological samples from tagged animals (for example, stable isotope analysis [135], genetic tests [136], physiological status studies [27,137]), or by experimentally manipulating tagged animals (for example, hormone manipulations [138], controlling feeding [139], cortisol injections [59]) or their environment (for example, temporary holding studies followed by release [140]).

Some of the earliest of such studies occurred on Pacific salmon in Japan and involved evaluating homing mechanisms [141] and the endocrinology of migration (reviewed in [142]). Recently, the first example of combining genomic studies with field telemetry of Pacific salmon identified the factors that are associated with migration failure in freshwater [143]. Integration of fish telemetry with detailed hydrodynamic studies has been used to optimize fish passage facilities through improved understanding of fish cognition and behaviour [144]. The number of such integrative studies appears to be increasing.

Data analysis tools and techniques

Following their development for terrestrial applications, many of the analytical techniques now being applied in marine systems were first applied in freshwater [145]. Of particular note is the use of mark-recapture models (and software for fitting models) for estimating detection, survival and state transitions during migration through rivers [146,147]. These papers adapted Cormack-Jolly-Seber and similar models (developed in the 1960s for survival through time) to salmon migration. More recently, survival analyses have been adapted for telemetry data from fishway assessments [148]. Voluminous amounts of data can be collected using telemetry but the advent of easy-to-use, computerized databases [149] has made it possible to organize and process data efficiently and present information in a highly useable form. Records of tag detections from many freshwater species have been entered into large databases managed by software such as ACCESS and HYDRA. The development of geographic information system (GIS) methods (for example, [150]), space-use analyses [151] and such computer programs as ARCVIEW, ARCINFO, RANGES and R has simplified and opened new possibilities for analyzing movement data in freshwater habitats. For example, fish telemetry data analyzed with home-range software led to important findings related to home-range establishment and shifts [152,153]. Nevertheless, most space-use analyses have been developed for terrestrial or marine applications and careful assessment of their applicability and bias is needed for the restricted and sometimes near-linear habitats of freshwater systems [154].

International collaborations

Although not unique to this field, there has been a notable increase in the number of freshwater telemetry studies in remote areas around the world, and also in many less economically developed countries. These efforts have contributed significantly to solving basic and applied research questions in regionally important freshwater animals, and have broadened the habitat types and animal taxa covered by such studies. As noted previously, given the threatened status of freshwater ecosystems and their animal

inhabitants, there is a great need for studies on fishes that support commercial and subsistence fisheries in less economically developed regions (for example, central Africa [62], the Mekong basin [155], the Amazon basin [48]). While biotelemetry has long been recognized as an important tool for freshwater research in these regions [156], its adoption has been driven by an apparent increase in available funding for international studies and collaborations, and for studies in developing countries, together with facilitation of such collaborations with the development of email communication and the internet, and greater affordability of equipment. Workshops have also been targeted towards building capacity for doing freshwater telemetry studies in less economically developed countries [157].

Future needs

The technical advances discussed in this paper have provided a strong foundation for the development of new technologies and technical innovations. Many of these advances will undoubtedly have an impact on the methods used to study aquatic animals and their surroundings. Although several emerging trends are evident in the literature (for example, advances in integrating and summarizing large data sets and the adaption of telemetry tools to novel species and environments), most can only be imagined. Here we provide an overview of what we regard as desirable future technical innovations and research needs related to the study of animals in freshwater systems (not ranked in any particular order). Most of these advances relate to transmitter design, tagging methods, tracking capabilities and tools for analyzing the large amounts of data collected. As in the past, many of the new technologies needed to overcome the constraints identified (Table 1) will probably come from advances in other fields that are then applied to fish and wildlife applications.

A major limitation with current telemetry systems is the size and functionality of the transmitters. Larger tags can provide increased reception range, operating life and sensor options, but limit the size of the individual and life stage that can be studied. Battery size is currently a limiting factor that dictates the ultimate size of the transmitter, the number and type of sensors that it can contain, and the duration of its longevity. Developing smaller, more efficient batteries to reduce transmitter size and increase operating life and reception range would help, but only to a limited degree. These technologies need to be combined with either hardware or software solutions that allow for more efficient power usage. Ultimately, more advanced tags will hopefully allow for near-lifetime tracking of large, long-lived animals from juvenile to adult in large freshwater systems (for example, large tropical catfishes).

While great strides have been made towards miniaturizing tags, there are limits to how far we can go with current technologies. In short, a technological wall has been reached that might significantly limit the extent to which we can study aquatic species. To that end, we preface this section by noting that in many ways we need a paradigm shift in the type of equipment we use to tag and track freshwater species. A component of this shift will be the development of tags that conserve battery power (to increase their lifespan and power peripheral sensors) until they are either required to collect data, or are transmitting data for collection. While not necessary for all applications, this transition will open up new avenues of research and innovation aimed at lifetime tracking of individual behaviour and environmental interactions. While the development of very small, long-lasting, inexpensive tags with a long range under a variety of environmental conditions remains an obvious but unlikely desire (dare to dream...), here we focus primarily on technical needs.

Environmental conditions

Given the extreme range of environmental conditions (for example, subarctic areas or tropical systems) that are home to freshwater species, adapting receiver technology for these conditions is essential. The production of field-ready (that is, waterproof, shock-proof) receiver housings would greatly expand the application of expensive telemetry equipment.

Sensors

While many sensors have been developed for a wide variety of applications, there are still areas where improvements to sensors or entirely new sensors would benefit the study of freshwater organisms. General improvements to both the reliability and ease of using complex sensors would make them more widely applicable. For example, while geolocation tags that use light or a magnetic field have produced valuable results, there is room to improve the algorithms used to derive their position. Reduced battery size has allowed for the development of PIT tags with simple sensors (for example, temperature). Further development of sensor and data storage PIT tags, as well as systems capable of transferring data from the tags, has great potential for large-scale studies. Work on this is ongoing in non-wildlife fields ([158]), but freshwater researchers should look to incorporate these technologies into their research.

While the concept has already been used in marine systems, freshwater animals may represent potentially useful bioprobes that can aid in environmental monitoring. A necessary component is the development of multisensor devices that provide spatial and environmental data that can be tracked over large spatial and

temporal scales. At the individual level, mortality tags have been developed that broadcast when an individual stops moving for a set amount of time. As tag sizes have decreased, prey species have increasingly been the focus of telemetry studies. With motion-sensing mortality tags, prey that has been consumed by a predator may still appear to be alive; therefore, development of a tag that senses when an individual has been eaten would provide a more accurate indication of mortality.

The combination of real-time, simultaneous, hydro-acoustic echo-sounding (horizontal or vertical) with interrogation of individuals with transmitters or transponders is a concept that dates back to Mitson and Storeton-West [159]. Given the numerous technological improvements since the 1970s, this approach should now be explored using state-of-the-art hydroacoustic equipment to simultaneously combine local-scale habitat and animal (especially fish) distribution and abundance to telemetered behaviour and ecophysiology of tagged individuals.

Archival tags

The major limitation associated with archival tags is the need to recapture tagged individuals to acquire stored data. A potential solution would be the development of archival tags with rapid download capability, probably downloaded as an individual moves through a remote gate. Since not all fish will pass near enough to such a structure, this design could be further improved through the addition of a 'chat' function that allows data to be exchanged between individuals and stored. This technology would be perfectly suited for species that are known to aggregate at some point in their lifecycle but may have low individual recapture rates (for example, adult sturgeon, which aggregate to spawn).

Although some large diadromous fish can be tagged with pop-up satellite archival transmitters (PSATs) in freshwater and pop-off transmitters in marine waters (for example, Atlantic sturgeon tagged in Hudson River [160]), there is a need for PSAT tags that function well in terms of both generating positions and 'popping-off' in freshwater. Presently, most pop-off assemblies are based on corrodible links that require a saline environment to degrade the attachment material, thereby limiting their application in freshwaters.

Tag transmission

Reception range, which should ideally be maximized due to the sizable areas typically associated with *in-situ* studies, is often marginal or inadequate. To expand the use of these studies to more complex environments, efforts should focus on improving monitoring systems that are capable of tracking animal movements in large, powerful river systems. Solutions will need to include overcoming underwater noise and improved deployment techniques

for acoustic telemetry equipment. To combat background noise that interferes with detections (a common problem in urban areas or near infrastructure, such as power plants), unique radiotelemetry coding systems could be developed or site-specific frequencies could be selected. Similarly, novel coding-schemes may help to improve the effectiveness of acoustic telemetry when species are located among macrophytes.

Passive integrated transponder (PIT) tags have been used successfully to study a variety of aquatic species under controlled settings, but the reception range (typically less than a metre) is insufficient for many studies in large, unconstrained environments. The development of more robust and powerful PIT systems and antennas that work in larger environments and under a broader range of environmental conditions will extend the application of PIT tags. Possible solutions include the further development of PIT trawls and meshless static PIT 'gill-nets' that detect tagged fish as they swim through them. In addition, when multiple PIT-tagged individuals pass through a stationary array, one tag may block the signal from another. The development of a method that prevents or circumvents this blockage is essential, to ensure that all individuals are detected.

For many telemetry studies, collecting large amounts of data is not a challenge. However, some variables (that is, continuous monitoring of depth or acceleration) are currently limited to archival storage tags. Advances in telemetric transfer and decoding of large or complicated datasets could expand the type of telemetry tags used for collecting continuous or long-term data. Similarly, enhanced telemetric transmission (in terms of rate and volume of data) would improve the transmission of video images (for example, 'critter cams') either in real time or using archival tags.

Tagging techniques

While a great deal of work has been directed towards improving tagging techniques (especially in fishes), further refinement of tagging procedures and validation of tagging techniques using the species being tagged (rather than surrogates [120]) are essential. This is particularly true for invertebrates, especially those that moult (for example, crustaceans). In addition to refining current techniques, there is also a niche for developing a rapid, internal tagging technique that can be used with aquatic vertebrates and large invertebrates (for example, development of injectable tags that are minimally invasive and require no anaesthetic).

Arrays

Two and three-dimensional arrays are one of the most promising new methods for tracking tagged individuals. Unfortunately, high costs and the complicated nature of

both the system themselves and the data they produce limit their broad application. A cheaper and more user friendly two- and three-dimensional system would open new possibilities and improve studies of detailed individual movements in areas above and below dams and through fishways or other possible migration barriers. One of the major challenges associated with two- and three-dimensional arrays is the overwhelming amount of data that can be acquired. To encourage the application of these arrays, data filtering and spatial location calculation methods need to be developed that can be easily applied, ideally by the scientist rather than the vendor. While passive telemetry systems have been installed in small lakes and both large and small rivers, there is a need for the development of large-scale communal telemetry systems at the scale of watersheds and entire lakes [27]. This would allow for ecosystem telemetry studies and manipulations of individuals in their entire natural environment.

Databases and analysis

A broad theme for all of the aforementioned future developments is to improve user interfaces and make them more readily accessible to nonexperts. This concept of user-friendliness also holds true for computer programs designed to organize and analyze large and cumbersome databases. Software improvements that allow users to integrate and summarize large databases easily would be a great asset, and built-in functions, such as analysis of home range, would be useful (especially in spatially complex environments). Also, from a statistical perspective, models are needed that estimate spatial movement processes and survival probabilities while accounting for observation errors. State-space models seem to have some promise, but a general model framework and software are lacking.

Collaboration

An important part of realizing the seven future needs that we have identified is the fostering of a strong relationship between users of telemetry equipment and those that design and produce it. These relationships have been and will be central to technological advances in freshwater telemetry. Early on, there were relatively few commercial vendors so most researchers either built their own equipment or worked with technical staff within their own agency or institution. Indeed, many of the first commercial suppliers were former researchers themselves, and the spirit of cooperation continued as they developed their product lines and became established. Although the quality of telemetry gear has vastly improved in recent decades, the importance of collaboration between suppliers and users remains paramount. Most equipment purchases

are based on predesigned items that may or may not be ideal. Many researchers assume that this is what is available and so make do, and vendors are often reluctant to make changes unless there is a clear upside for sales. Although this is understandable from an economic standpoint, it is not conducive to advancing the technology in a field where funding is often limited. Collaboration between field researchers and product designers and manufacturers is likely to be a key factor in relation to the utility and effectiveness of future advances.

Conclusion

Over the years, advances in electronic tags have had a significant impact on the ability to study aquatic animals under a variety of challenging conditions. Here, we reflected on the history of these advances and, in doing so, we were able to characterize the key technical developments that have made electronic tags such a useful tool in research. Most research activities and innovation have arisen from work on fish, but there is certainly an opportunity for greater application of such technology to other taxa and to smaller animals including invertebrates and amphibians.

Many constraints make the use of electronic tags challenging, but for most applications there is at least one form of technology that will work. The reality is that technological limitations require researchers to make trade-offs, which necessitates preparation of clear research questions and research priorities during the study design process. Different research questions may require the application of very different technologies. Compared to where the field was 50 years ago, we have come a long way. Innovations continue, as summarized here, but there are still a variety of future needs that, if achieved, could open more doors for studying freshwater animals. Electronic tag practitioners and equipment manufacturers need to work closely if such advances are to be meaningful and rapid. However, not all of those needs are purely technological, as continued work is needed on analytical and statistical procedures to handle the large volumes of data generated. Further, efforts to refine and validate tagging procedures to ensure that the data are representative of untagged conspecifics and that the welfare status of tagged animals is maintained, are still needed. Many meaningful gains in conservation and management will likely be ascribed to electronic tagging innovations in freshwater in the next 10 to 20 years, and we expect novel discoveries relating to fundamental animal and environmental biology. Indeed, with the growing threats facing freshwater ecosystems and their fauna, the need for further technical and technological improvements is urgent if the scientific community is to provide the data needed to inform conservation efforts.

Abbreviations

CART: Combined acoustic radio transmitter; CDMA: Code division multiple access; CHAT: Communicating histogram acoustic transponder; GIS: Geographic information system; GPS: Global positioning system; HF: High frequency; PIT: Passive integrated transponder; PSAT: Pop-up satellite tag; SPOT: Smart position-only tag; USGS: United States Geological Survey; VHF: Very high frequency.

Competing interests

The authors declare that they have no competing interests.

Authors' contributions

All authors helped to identify important historical developments, current constraints and future needs for freshwater biotelemetry in their specific areas of expertise. In addition, JDM helped to synthesize these contributions and SJC wrote the initial draft of the manuscript. All authors were also involved in subsequent revisions of the manuscript. All authors read and approved the final manuscript.

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Author details

¹Fish Ecology and Conservation Physiology Laboratory, Department of Biology, Carleton University, 1125 Colonel By Dr., Ottawa, ON, Canada. ²Biotelemetry Laboratory, Department of Fish, Wildlife and Conservation Biology, University of California at Davis, Davis, CA, USA. ³Aquatic Animal Ecology Research Group, School of Biological and Biomedical Sciences, Durham University, Durham, UK. ⁴Norwegian Institute for Nature Research, Trondheim, Norway. ⁵Auke Bay Laboratories, Alaska Fisheries Science Center, National Marine Fisheries Service, National Ocean and Atmospheric Administration, Juneau, AK, USA. ⁶Hammond Bay Biological Station, United States Geological Survey, Millersburg, MI, USA. ⁷Tropical Landscapes Joint Venture, CSIRO Ecosystem Sciences & TropWATER, James Cook University, Atherton, QLD, Australia.

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